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Resting state networks and memory consolidation

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Despite their name, resting state networks (RSNs) provide a clear indication that the human brain may be hard-working. Unlike the cardiac and respiratory systems, which greatly reduce their rate of function during periods of inactivity, the human brain may have additional responsibilities during rest. One particularly intriguing function performed by the resting brain is the consolidation of recent learned information, which is known to take place over a period of several hours after learning. We recently reported that resting state brain activity is modulated by recent learning. We measured the brain activity using functional MRI during periods of rest that preceded and followed learning of a sensorimotor task, and found a network of brain areas that changed their resting activity. These areas are known to be involved in the acquisition and memory of such sensorimotor tasks. Furthermore, the changes were specific to a task that required learning, and were not found after motor performance without learning. Here we discuss the implications and possible extensions of this work and its relevance to the study of memory consolidation.

Key words: learning, motor skill, RSN, slow-wave sleep, motor learning, memory maintenance, memory persistence

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The human brain has a high metabolic demand, and much of this energy is used to sustain spontaneous synaptic processing.[1] Such resting activity is not random; instead, there are highly organized patterns of coherent activity.[2] So while most functional neuroimaging experiments are based on detecting temporal correlations between brain signals and known input stimuli or output behaviors, newer analytical techniques allow identification of spatial networks defined only by their within-network correlations, unrelated to external events. This makes possible the identification of "resting state" brain systems without defining their time-course. The pattern of correlated activity defines specific segregated networks which are consistent across studies and even remain under sedation or during sleep.[3-5]

The function of such activity remains poorly understood but absence of a time-locked brain-behavior relationship does not preclude meaningful relationships between resting brain functions and behaviour. For example, spontaneous resting activity within the primary motor cortex can predict future response times to external stimuli.[6] Thus, resting activity may make the human brain highly responsive to external events, and so the resting brain affects our future behavior. Recently, we set out to examine the reciprocal relationship: the capacity for earlier behaviors to affect subsequent resting brain activity, and so in turn develop a deeper understanding of the resting brain.

Memory in the Resting Brain

We measured spontaneous patterns of activity within the resting brain before and after learning a new sensorimotor skill or sensorimotor performance, and showed that two circuits within the resting brain were specifically affected by sensorimotor learning.[7,8] One included the frontal and parietal cortices, the other included the bilateral cerebellum. Both of these circuits have been implicated in sensorimotor learning,[9-11] and it may be that these same areas continue to be engaged during memory consolidation processes that occur

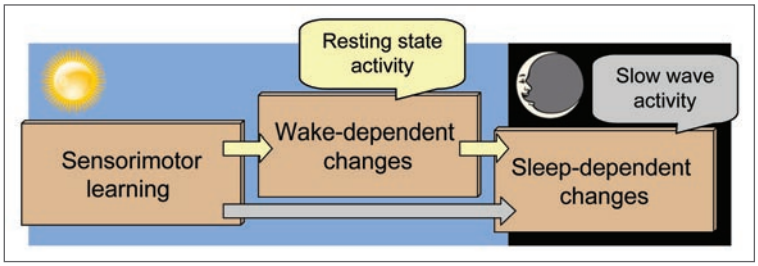

Figure 1. Consolidation across the day. Contributions of resting-state and slow-wave activity to memory consolidation may be differentiated based upon the times at which they occur—with resting-state networks supporting consolidation prior to the onset of sleep.

during the "off-line" period between performances. Unfortunately, in our recent work a measure of consolidation was never taken, and so within-group correlations between the amount of consolidation and the extent of the resting state changes were not possible. Nonetheless, we showed that the resting brain was affected by prior sensorimotor learning, and not by the mere performance of a sensorimotor skill, making an important connection between neuroplastic changes induced by learning and the resting brain. This is a necessary first step towards testing the idea that spontaneous resting activity is responsible for the off-line processing of memories during consolidation.[12]

Identifying Task-Specific and Task-Independent Memory Consolidation Systems

Two circuits within the resting brain were affected by prior sensorimotor learning,[7] and some have suggested that two circuits underlie motor skill consolidation.[13] Our results may provide additional evidence for these dissociable consolidation systems. We found no learning related modulation of primary motor cortex (M1), which has been shown to make a critical contribution to consolidation of simple motor skills.[14,15] It may be the case that the challenging visuomotor task learned in our experiment depends on consolidation within fronto-parietal circuits and does not require the contributions of M1.[16] Future work might usefully distinguish between those circuits that are differentially related to the consolidation of different types of skills—or even underlie the consolidation of other forms of memory—semantic or episodic—or learning (e.g., sequential or perceptual tasks).

Resting State and Brain State

Memory consolidation can occur over wakefulness; but, some consolidation can only occur over sleep.[10,13] Current theory suggests that anatomically distinct circuits support wake-dependent and sleep-dependent consolidation.[13,17] One prediction from this theory is that two distinct circuits within the resting brain should be affected by prior sensorimotor skill learning.[7] It may be the case that resting state changes within one of these sensorimotor circuits correlates with wake-dependent performance changes;[7,18] whereas, changes within the other circuit could correlate with sleep-dependent performance changes (Fig. 1). So our data might indicate that the fronto-parietal circuit is supporting memories that will undergo sleep-dependent consolidation, whereas the cerebellum is supporting memories undergoing wake-dependent consolidation. This hypothesis must be tested. Others have observed that increases in slow-wave activity (SWA) occur over the parietal cortex during sleep.[19] It may be that changes in spontaneous activity during wakefulness are responsible for triggering the subsequent increases in SWA during sleep. SWA appears to lead to synaptic modulations which may be a key mechanism for sleep-dependent consolidation.[19] This concept predicts that spontaneous resting state activity within the parietal cortex during wakefulness may be correlated with parietal SWA changes during sleep. Showing such a correlation would provide a strong link between the resting and the sleeping brain.

Changes within the resting brain may also occur as the circuits responsible for the initial encoding of a memory are reactivated for the consolidation of the memory.[20] Recent work has shown that memories can be reactivated during wakefulness,[21] and such neuronal replay may be delayed in other circuits until the onset of sleep when reactivation is thought to play a critical role in sleep-dependent consolidation.[22-27]

So learning, as our recent work shows, affects spontaneous activity within the resting brain. Understanding exactly how that resting activity is affected may provide insight into the mechanisms and pathways responsible for determining how memories consolidate over wakefulness or over sleep.

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